

***Daedalochila* sp. nov. from northwest Arkansas, U.S.A., the anatomy of the *Polygyra plicata* group, and the validity of the genus *Millerelix* Pratt, 1981 (Gastropoda: Pulmonata: Polygyridae)**

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Abstract: The species of the *Polygyra plicata* group Pilsbry, 1940 of the Polygyridae, Polygyrini - *Polygyra plicata* Say, 1821; *Polygyra dorfeuilliana* Lea, 1838; *Polygyra fatigiata* Say, 1829; *Polygyra jacksoni* (Bland, 1866); *Polygyra peregrina* Rehder, 1932; and *Polygyra troostiana* Lea, 1839 - have been placed in the genus *Millerelix* Pratt, 1981 on the basis of limited anatomical data. We present the genital anatomy of these species and describe a new species from the Ozark uplift of Arkansas, U.S.A., *Daedalochila bisontes* sp. nov. The new species is similar to *P. peregrina*. It is distinguished by its smaller size, more closely coiled and weakly striate shell, and by the structure of the lamellae of the apertural lip. The parietal lamella bears a prominent angled projection apically and an obtuse angle basally. The palatal lamella is deeply immersed and long, curving inwards and downwards towards the basal lamella, sinuous and undulate, appearing in apertural view as two overlapping lamellae. The diagnostic character of *Millerelix* was not consistently present in the *Polygyra plicata* group; i.e., the pendant, conical projection in the apical penis was observed only for *P. plicata* itself and not confirmed for *P. dorfeuilliana*. The diagnostic characters of *Millerelix* (*Prattelix*) Emberton, 1995 and *Millerelix* (*Millerelix*) were also found to be unreliable; i.e., a thickened proximal vas deferens was found in all 6 species and the width/length of the penis (0.10-0.18) was similar in *Polygyra* (*Millerelix* [*Millerelix*]) *dorfeuilliana* and *Polygyra* (*Millerelix* [*Prattelix*]) *plicata*. *P. troostiana* and *P. fatigiata* possess penises of greater width/length (~0.36) and lack any trace of an epiphallus, features that appear to place them (anatomically) close to *Daedalochila* (*Upsilidon*) Pilsbry, 1940. Because of the variability of these features, *Millerelix* Pratt, 1981 is not maintained, and the species of the *Polygyra plicata* group are referred to the senior genus *Daedalochila* Beck, 1837.

Key words: endemism, genital morphology, Ozark uplift, taxonomy

The *Polygyra plicata* group was established by Pilsbry (1940) for the Polygyrinae of the Cumberland plateau and Ozark uplift of the southern U.S.A., i.e., *Polygyra plicata* Say, 1821; *Polygyra dorfeuilliana* Lea, 1838; *Polygyra fatigiata* Say, 1829; *Polygyra jacksoni* (Bland, 1866); *Polygyra peregrina* Rehder, 1932; and *Polygyra troostiana* Lea, 1839. Pilsbry (1940) gave no formal rank to the group, placing the species in the (then) subgenus *Daedalochila* Beck, 1837. The group remained without a formal name until the most recent revision of the Polygyridae by Emberton (1995), who extended the concept of the genus *Millerelix* Pratt, 1981 (originally erected for several Texan species of Polygyrini [Pratt 1981a, 1981b]) to include all members of the *Polygyra plicata* group. *Millerelix* has been used in this sense by subsequent workers (Turgeon *et al.* 1998).

During field work on the distribution of land snails in Arkansas, U.S.A. (Coles and Walsh 1999, Walsh and Coles 2002), a polygyrid snail of the *Polygyra plicata* group was found that was distinct from other related species, although superficially similar to *Polygyra peregrina* of the same region. When the anatomy of the new form was studied, it became apparent that it did not conform to the diagnostic genital characters of the genus *Millerelix*, either as defined by Em-

berton (1995) to include the entire *Polygyra plicata* group or as originally described by Pratt (1981a, 1981b).

To gain more insight into the validity of the concept of a single genus to describe the members of the *Polygyra plicata* group, we describe the new Arkansas species and present dissections of all the species within the group. In particular, we present illustrations of the internal features of the penis because these have been used by both Pratt (1981a, 1981b) and Emberton (1995) as diagnostic generic characters (Table 1) but have not been illustrated, even for those few species for which the anatomy is known.

MATERIALS AND METHODS

Specimens of Polygyridae were collected as part of our studies on the distribution of land molluscs of Arkansas, Tennessee, and Alabama. The identities of the species were ascertained by reference to Pilsbry (1940) and the collections of the Field Museum of Natural History, Chicago (FMNH). Additional specimens of the new species were located in the Hubricht collection at the FMNH and the Causey collection at the University of Arkansas Museum, Fayetteville (UAF). Live specimens of all members of the *Polygyra plicata* group

Table 1. Characters used to define genera and subgenera within the *Millerelix*/*Daedalochila* clade and the species assigned to the genera/subgenera by Emberton (1995).

Genus (Subgenus)	Characters (character set of Emberton 1995: 77)	Species ¹
<i>Millerelix</i>	A slender penis (width ≤ 0.12 length) with an apical, pendant, conical projection, and derivatives thereof (87).	
(<i>Millerelix</i>)	An extremely long and slender penis (width < 0.06 length) (88).	<i>mooreana</i> , <i>dorfeuilliana</i> , <i>gracilis</i> ² , <i>?implicata</i> , <i>lithica</i> , <i>?rhoadsi</i> , <i>tholus</i> .
(<i>Prattelix</i>)	A greatly enlarged, muscular, proximal vas deferens (89).	<i>plicata</i> , <i>deltoidea</i> ³ , <i>fatigiata</i> , <i>jacksoni</i> , <i>peregrina</i> , <i>plicata</i> , <i>simpsoni</i> ³ , <i>troostiana</i> .
<i>Daedalochila</i>	Even-diameter vas deferens with no trace of epiphallus (90).	
(<i>Upsilonidon</i>)	A stout penis (length/diameter < 3.5 [diameter/length > 0.29]) with a straight apex (91).	<i>hippocrepis</i> , <i>?acutedentata</i> , <i>burlesoni</i> , <i>chisosensis</i> , <i>dalli</i> , <i>leporina</i> , <i>multiplicata</i> , <i>?poeyi</i> , <i>sterni</i> .
(<i>Daedalochila</i>)	A moderately long penis ($4 < \text{length/diameter} < 10$ [$0.1 < \text{diameter/length} < 0.25$]) with a bent or convoluted apex (92). A downward curve on the lower limb of the parietal apertural denticle (93). A raised parietal callus (94).	<i>auriculata</i> , <i>?ariadne</i> , <i>auriformis</i> , <i>avara</i> , <i>delecta</i> , <i>hausmani</i> , <i>?oppiliata</i> , <i>peninsulæ</i> , <i>postelliana</i> , <i>subclausa</i> , <i>uvulifera</i> .

¹ The type species is given first, in bold (for author citations see text and below).

² Regarded as a form of *mooreana* by some workers (cf. Pratt 1981b). ? indicates species provisionally assigned.

³ Regarded as forms of *jacksoni* by Pilsbry (1940).

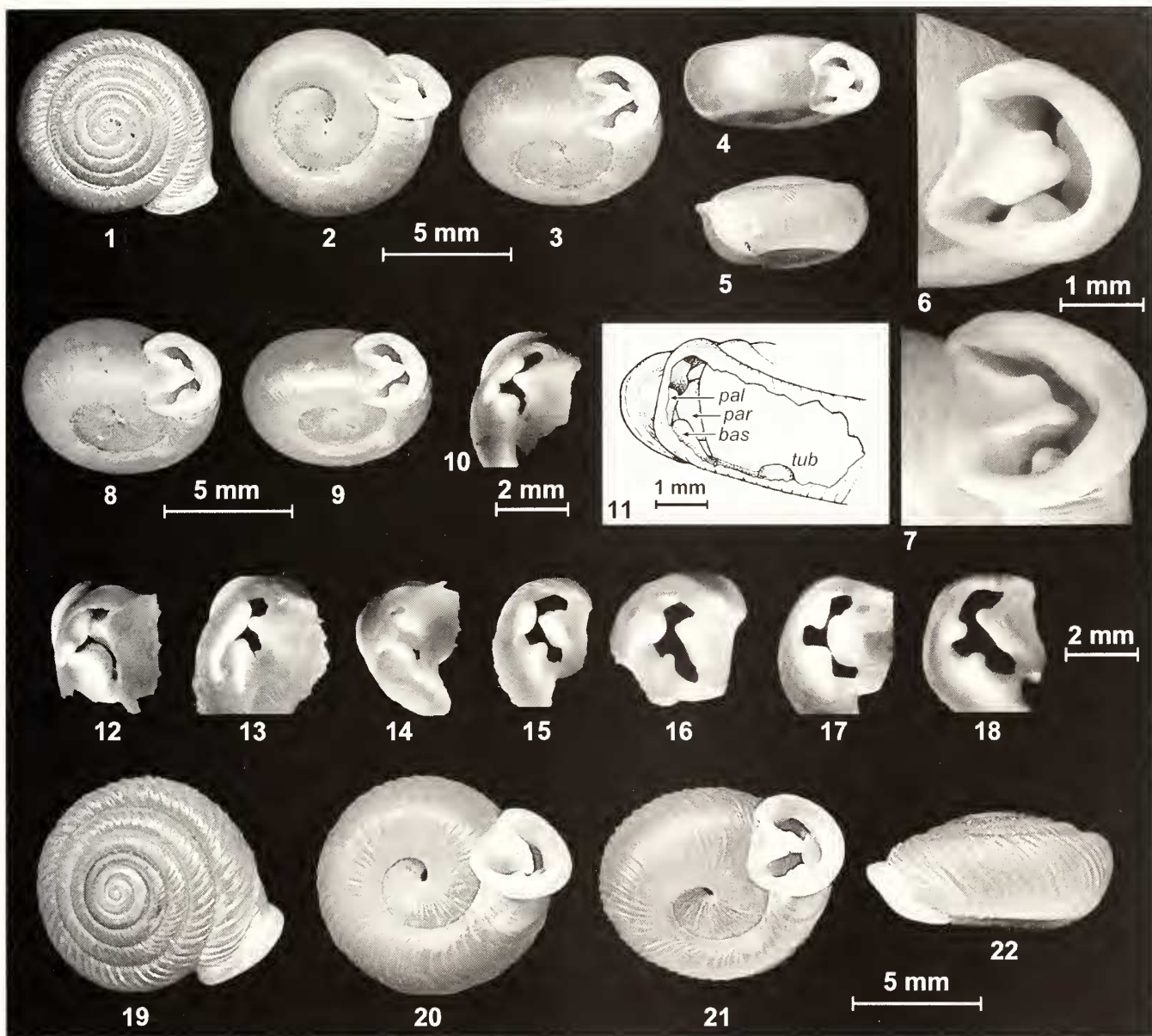
Author citations for species not otherwise referred to in the text are as follows. *Millerelix* (*Millerelix*) *implicata* (Martens, 1865); *Millerelix* (*Millerelix*) *rhoadsi* (Pilsbry, 1900); *Millerelix* (*Millerelix*) *tholus* (Binney, 1857); *Millerelix* (*Prattelix*) *deltoidea* (Simpson, 1889); *Millerelix* (*Prattelix*) *simpsoni* (Pilsbry and Ferriss, 1907). *Daedalochila* (*Upsilonidon*) *hippocrepis* (Pfeiffer, 1848); *Daedalochila* (*Upsilonidon*) *acutedentata* (Binney, 1858); *Daedalochila* (*Upsilonidon*) *burlesoni* (Metcalf and Riskind, 1979); *Daedalochila* (*Upsilonidon*) *chisosensis* (Pilsbry, 1936); *Daedalochila* (*Upsilonidon*) *dalli* (Metcalf and Riskind, 1979); *Daedalochila* (*Upsilonidon*) *leporina* (Gould, 1948); *Daedalochila* (*Upsilonidon*) *multiplicata* (Metcalf and Riskind, 1979); *Daedalochila* (*Upsilonidon*) *poeyi* (Aguayo and Jaume, 1947); *Daedalochila* (*Upsilonidon*) *sterni* (Metcalf and Riskind, 1979); *Daedalochila* (*Daedalochila*) *auriculata* (Say, 1818); *Daedalochila* (*Daedalochila*) *ariadne* (Pfeiffer, 1848); *Daedalochila* (*Daedalochila*) *auriformis* (Bland, 1862); *Daedalochila* (*Daedalochila*) *avara* (Say, 1818); *Daedalochila* (*Daedalochila*) *delecta* (Hubricht, 1976); *Daedalochila* (*Daedalochila*) *hausmani* (Jackson, 1948); *Daedalochila* (*Daedalochila*) *oppiliata* (Morelet, 1849); *Daedalochila* (*Daedalochila*) *peninsulæ* (Pilsbry, 1940); *Daedalochila* (*Daedalochila*) *postelliana* (Bland, 1862); *Daedalochila* (*Daedalochila*) *subclausa* (Pilsbry, 1899); *Daedalochila* (*Daedalochila*) *uvulifera* (Shuttleworth, 1852).

were obtained during these studies. Specimens were drowned overnight in sealed containers of degassed (boiled and cooled) water and preserved in 70% ethanol.

Images of the entire shell were obtained using a Hewlett Packard Scanjet 4C at a resolution of 600 dpi (Figs. 1-5, 8-9, 19-22). Shells were laid directly on the scanner platten or fixed at a desired angle using a probe. Images (as TIFF files) were adjusted empirically for contrast and brightness (and also to remove the image of the probe) using Adobe Photoshop®. Details of the aperture (Figs. 6-7) were obtained by scanning electron microscopy (SEM), using a Hitachi S-2460N, with AC voltage at 22 kV in N-SEM mode at 10 Pa vacuum. The shell was not coated with heavy metal. For details of these specimens see legend to Figs. 1-22.

Views of the apertural lamellae of the shell from behind the aperture (Figs. 10, 12-18) were obtained by removing pieces of the shell from behind the aperture until a clear view of the lamellae was possible. The resultant apertural fragments were placed aperture-down on the base of a Zeiss SM2U dissecting microscope attached to a MTI DCC30

digitizing camera. Lighting was adjusted empirically until the best views of the lamellae were obtained. Images were acquired using FlashPoint and adjusted for contrast and brightness using Adobe Photoshop®. The specimens were: *Daedalochila bisontes* sp. nov. (Fig. 10), type locality, B. Coles, 8 May 1999 (FMNH293229); *Daedalochila jacksoni* (Fig. 12), Arkansas, Franklin County, Reed Mountain Park, Ozark, B. Coles, 18 January 1999 (FMNH293235); *Daedalochila peregrina* (Fig. 13), Arkansas, Searcy County, Highway 65 at junction with highway 74, 5 miles N of Marshall, B. Coles, 3 May 1998 (FMNH293231); *Daedalochila plicata* (Fig. 14), Tennessee, Van Buren County, Bone Cave Mountain 5 miles NE of Spencer, B. Coles, 20 June 1996 (FMNH293237); *Daedalochila troostiana* (Fig. 15), Tennessee, De Kalb County, Cove Hollow Road at N end of Center Hill Lake, B. Coles, 16 April 1999 (FMNH293243); *Daedalochila fatigiata internuntia* (Fig. 16), Tennessee, Perry County, Perryville, Mousetail Landing State Park, B. Coles, 23 March 2000 (FMNH293244); *Daedalochila dorfeuilliana* (Fig. 17), Arkansas, Hempstead county, Saratoga Landing, B.



Figures 1-22. Shell characters of *Daedalochila bisontes* sp. nov. and related species. Figs. 1-5, *D. bisontes*, flat-bed scans of the holotype (FMNH287396). Figs. 6-7, *D. bisontes*, SEMs of the aperture of the holotype. Figs. 8-9, *D. bisontes*, flat-bed scans of two paratypes (FMNH293226). Fig. 10, *D. bisontes*, apertural fragment showing detail of lamellae viewed from behind the aperture (FMNH293229). Fig. 11, *D. bisontes*, sketch of shell opened behind aperture to show the appearance of the palatal lamella (*pal*) as two overlapping lamellae and the tubercle (*tub*) on the umbilical axis. Figs. 12-18, apertural fragments of shells of the *Polygyra plicata* group and related species viewed from behind the aperture: Fig. 12, *Daedalochila jacksoni*; Fig. 13, *Daedalochila peregrina*; Fig. 14, *Daedalochila plicata*; Fig. 15, *Daedalochila troostiana*; Fig. 16, *Daedalochila fatigiata internuntia*; Fig. 17, *Daedalochila dorfeuilliana*; Fig. 18, *Daedalochila moorcana*. Figs. 19-22, *Daedalochila peregrina*, flat-bed scans (Arkansas, Calico Rock, Stone County [FMNH293232]). Views of entire shells are at the same scale (scale bar = 5 mm). For views of apertural fragments, scale bar = 2 mm; for SEMs scale bar = 1 mm. For apertural fragments, the orientation of the lamellae is shown on Fig. 11, otherwise, shells are viewed in the conventional way with the parietal lamella to the left and palatal lamella to the right. Abbreviations: *bas*, basal lamella; *pal*, palatal lamella; *par*, parietal lamella.

Coles, 5 January 2003 (FMNH293239); *Daedalochila mooreana* (Fig. 18), Texas, Comal County, bluffs of Guadalupe River, approximately 6 miles W of New Braunfels, B. Coles, 24 December 1997 (FMNH293246).

Shell measurements were taken using vernier calipers. Shell diameter and height were measured as described by Pilsbry (1939). Measurements were taken at least twice and the average used. Replicate measurements were within ± 0.05 mm. Whorls of the spire were counted (at 4X magnification) as described by Pilsbry (1939) and umbilical whorls counted similarly, using the central umbilical hole as the starting point; accuracy was to ± 0.05 whorl. Measurements were taken of 126 specimens of *Daedalochila bisontes*, including the holotype, unbroken paratypes, and other material marked with an asterisk (*) in *Paratypes* and *Other Material* and 144 specimens of *Daedalochila peregrina*; that is, 58 shells from Calico Rock, Stone County, B. Coles, 16 April 1995 (FMNH293233); 49 shells from Allison, Stone County, B. Coles, 28 February 1999 (FMNH293234), and 37 shells from Searcy County, Highway 65 at junction with Highway 74, 5 miles N of Marshall, B. Coles, 21 April 2002 (FMNH293232). These data were analyzed by box plots, simple graphical plots, and by comparison of means for significant differences by Student's t-test using the programs SigmaStat and SigmaPlot.

Dissections were performed at 20-40X magnification. The shell was removed from the body, the animal opened from near the genital pore to the lung, and the tissues teased apart while submerged in 70% ethanol. The right ocular retractor muscle was cut and partially removed to aid viewing the basal penis. The penis was opened with a sharpened spear-point needle from near its junction with the atrium/vagina to the epiphallus or to the attachment of the penial retractor muscle (or as far as the fragility of the tissues would allow). Sections of the penis were obtained by cutting the opened penial tubes where indicated in the figures and allowing the remaining tissues to reform to their approximate original cylindrical forms. Drawings were made by eye, taking particular care to ensure that relative proportions of the organs were accurately reproduced, and with reference to an appropriate scale.

The nomenclature used for the apertural lamellae (equivalent to the apertural "teeth" or "denticles" of other authors) and the concordance with the nomenclature of Pilsbry (1940) in parentheses, is as follows: parietal lamella (parietal tooth), palatal lamella (outer lip tooth), basal lamella (basal lip tooth). Abbreviations are used as follows: Buffalo National River (BNR), Carnegie Museum of Natural History (CM), Field Museum of Natural History (FMNH), Florida Museum of Natural History (UF), University of Arkansas Museum Fayetteville (UAF).

SYSTEMATICS

Class GASTROPODA

Subclass PULMONATA

Order STYLOMMATOPHORA

Family POLYGYRIDAE Pilsbry, 1894

Subfamily POLYGYRINAE

Tribe POLYGYRINI

Genus *Daedalochila* Beck, 1837 [*non Daedalochila sensu* Emberton, 1995]

Polygyra plicata group Pilsbry, 1940

Daedalochila bisontes sp. nov.

[undescribed *Millerelix* sp. nov. Coles and Walsh 1999, Walsh and Coles 2002]

Figs. 1-11, 23-25, 40-41

Diagnosis

A medium-sized species of the *Polygyra plicata* group, similar in aspect to *Daedalochila peregrina*; depressed-discoidal, weakly rib-striate above, umbilicus perforate expanding to approximately 2/3 diameter of shell, forming an almost planar spiral; shell aperture with three lamellae; parietal lamella triangular-quadrate, a prominent angled projection apically and obtuse angle basally; palatal lamella deeply immersed and long, curving inwards and downwards towards the basal lamella, sinuous and undulate, appearing in apertural view as two overlapping lamellae; a tubercle on the umbilical axis approximately 1/4 whorl inside body whorl.

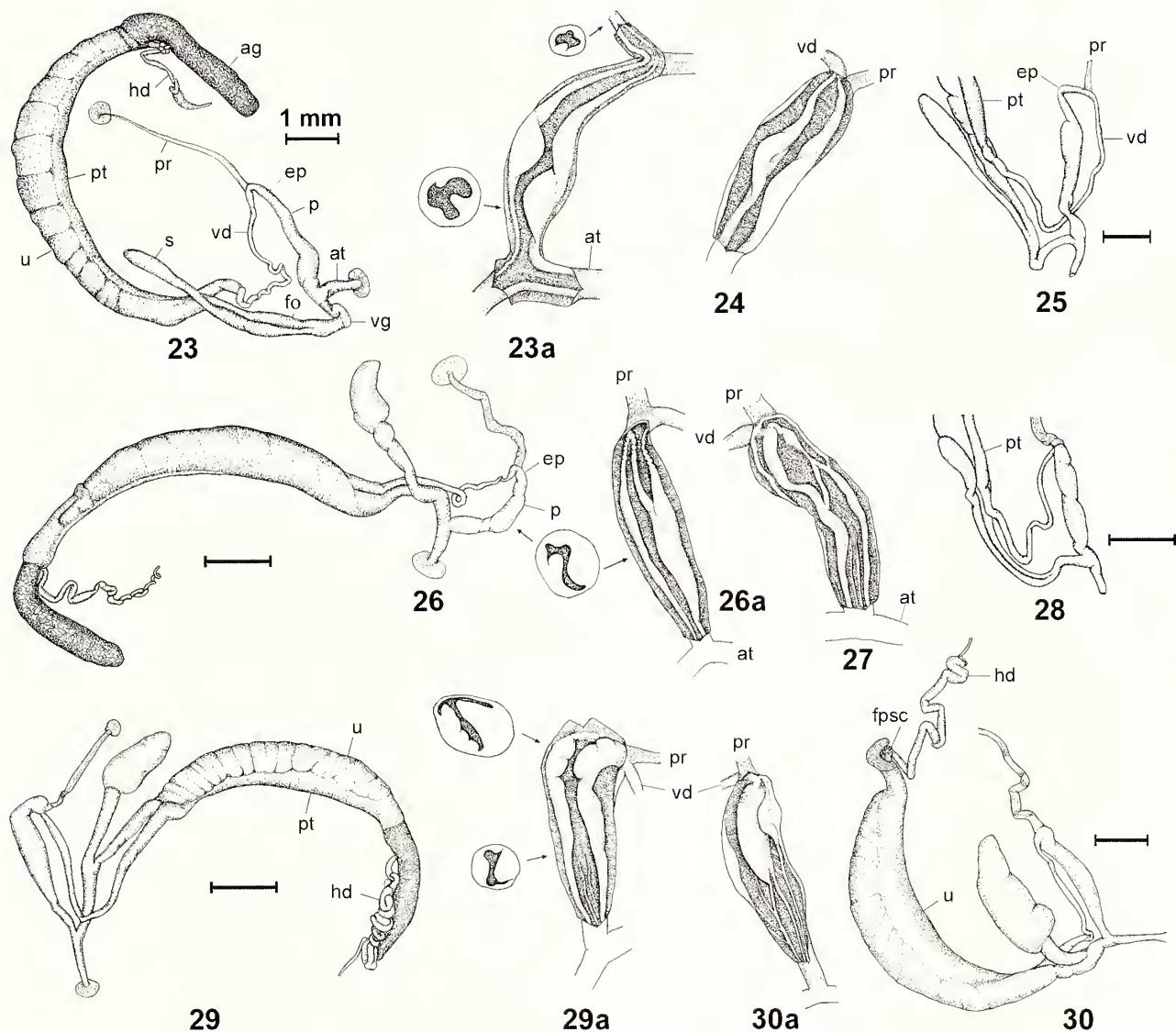
Holotype (Figs. 1-7)

FMNH287396, preserved dry: U.S.A., Arkansas, Searcy County; Leslie, approximately 1 mile S of town center, just within city limits, opposite stone quarry yard, a roadside bank with limestone outcrops on W side of Highway 65, on soil under kudzu and other herb cover; B. Coles, 13 May 1998.

Paratypes (* indicates measured).

Arkansas, Madison County: UAF95-1-330 (Causey Collection), 5 specimens preserved dry: Denny's Cave, Huntsville, Etgay (no initials given), May 1954.

Arkansas, Searcy County: *FMNH287397, 29 specimens preserved dry: collected with holotype. *FMNH293226, 2 specimens preserved dry (Figs. 8-9): collected with holotype. FMNH287398, 6 specimens preserved in alcohol: collected with holotype. FMNH287399, 4 specimens dissected and preserved in alcohol: collected with holotype. FMNH293227, 4 specimens dissected, preserved in alcohol: type locality, B. Coles, 8 May 1999. FMNH293229, 1 apertural fragment (Fig. 10): type locality, B. Coles, 8 May 1999. FMNH255872, 5 specimens preserved dry: 2 miles SE of Marshall, L. Hu-



Figures 23–30. Genital anatomy of *Daedalochila bisontes*, *Daedalochila peregrina*, and *Daedalochila jacksoni*. Fig. 23, *Daedalochila bisontes* sp. nov., genitalia of a specimen with weakly differentiated epiphallus; Fig. 23a, the penis of the same specimen opened from the vagina/atrium to the vas deferens, insets show sections of the penis and vas deferens. Fig. 24, *D. bisontes*, opened penis of a second specimen. Fig. 25, *D. bisontes*, distal genitalia of a third specimen showing well-defined and bent epiphallus. Fig. 26, *Daedalochila peregrina*, genital anatomy; Fig. 26a, opened penis and penial section (inset) of the same specimen. Fig. 27, *D. peregrina*, opened penis of a second specimen. Fig. 28, *D. peregrina*, distal genitalia of a third specimen. Fig. 29, *Daedalochila jacksoni*, genital anatomy; Fig. 29a, opened penis and penial sections (insets) of the same specimen. Fig. 30, *D. jacksoni*, distal genital anatomy of a second specimen; Fig. 30a, opened penis of the second specimen showing pilasters weakly developed basally. Scale bars are all 1 mm and refer to the gross genitalia only. Abbreviations: ag, albumin gland; at, atrium; ep, epiphallus; fo, free oviduct; fpse, fertilization pouch-seminal receptacle complex; hd, hermaphrodite duct; p, penis; pr, penial retractor muscle; pt, prostate gland; s, spermatheca; u, uterus; vd, vas deferens; vg, vagina.

bricht, 31 July 1955. FMNH293228, 1 specimen dissected, plus 1 entire, preserved in alcohol: Leslie, Kiwanis Road, B. Coles, 21 April 2002. *UF278302, 8 specimens preserved dry: type locality: J. Slapcinsky and B. Coles, 8 May 1999. UF278303, 4 specimens preserved in alcohol: type locality, J. Slapcinsky and B. Coles, 8 May 1999. *UF278317, 23 speci-

mens preserved dry: Leslie, County Road 9 (Kiwanis road), J. Slapcinsky and B. Coles, 8 May 1999. *CM65377, 10 specimens preserved dry: Leslie, type locality, B. Coles, 13 May 1998.

Arkansas, Newton County: FMNH255871, 3 specimens preserved dry: 12 miles S of Jasper, L. Hubricht, 29 April 1936.

Arkansas, Stone County: FMNH287400, 3 specimens preserved dry: 5 miles N of Allison, L. Hubricht, 9 February 1960.

Other material (* indicates measured).

Arkansas, Newton County: Two specimens: Carver, Gene Rush-Buffalo River Wildlife Management Area, 1 mile E of Highway 123, B. Coles, 1 May 1998. 17 Specimens: Center Point Trail, Buffalo National River (BNR), G. Walsh, 23 May 1997. *4 specimens: Lost Valley Trail BNR, G. Walsh, 23 September 1996. *10 Specimens: Hemmed in Hollow, BNR, G. Walsh, 17 June 1997.

Arkansas, Searcy County: *25 Specimens: Leslie type locality, B. Coles, 8 May 1999. 19 Specimens: Leslie, Kiwanis Road, B. Coles, 7 May 1998 and 21 April 2002. 3 specimens: Marshall, Highway 65, 2 miles SE of town, B. Coles, 16 May 1998 and 8 May 1999. 10 specimens: Tyler Bend, River View Trail, BNR, G. Walsh, 30 September 1995. 3 specimens: Tyler Bend, Spring Hollow Trail, BNR, G. Walsh, 30 September 1995. *18 specimens: Tyler Bend, Center Point, Buffalo River Hiking Trail BNR, G. Walsh, 10 January 1995.

Description

Shell (Figs. 1-9) mid - light brown, discoidal, diameter 6.15-7.96 mm (mean 7.14 mm, holotype 7.35 mm); height 2.50-3.31 mm (mean 2.89 mm, holotype 2.67 mm). Closely wound; whorls 5.25-6.20 (mean 5.73, holotype 5.80); spire low; periphery rounded; umbilicus perforate, expanding to form an open almost planar spiral; umbilical whorls 1.00-1.60 (mean 1.25, holotype 1.25), umbilicus (between sutures) approximately 1/2 maximum shell diameter. Embryonic sculpture of weak axial striae, subsequently weakly rib striate, the rib-striae becoming obsolete as they cross the periphery, but stronger behind the aperture. Shell aperture rounded; peristome strongly thickened, reflected, ends connected by a low parietal callus appressed to the body whorl, porcellaneous, appearing slightly rough at 40X magnification (Figs. 6-7). Aperture bears parietal, basal, and palatal lamellae. Parietal lamella triangular-quadrate in apertural view, a prominent projection approximately midway on apical surface, an obtuse angle basally. The basal lamella emerges onto the lower peristome and extends approximately 0.1 whorls into the body whorl. The palatal lamella is deeply immersed and long, curving inwards and downwards towards the basal lamella, sinuous and undulate (Figs. 10-11), appearing in apertural view as two overlapping lamellae. Internally, there is a tubercle on the umbilical axis approximately 1/4 whorl inside the body whorl (Fig. 11). Unworn (young adult) shells possess sparse short (approximately 0.5 mm long) periostracal hairs primarily on the basal surface.

Genital anatomy

Nine specimens were dissected from the type locality

(FMNH 287399, FMNH293227, FMNH293228); the penis opened in two specimens (Figs. 23-25). Atrium approximately 1/4 the length of the penis, vagina approximately twice as long as the atrium, strongly reflexed mid-way. Free oviduct to the bend in the vagina approximately the same length as the penis, 2-3 mm long. Penis elongate, approximately 2.5 mm in length variably swollen at mid-length, maximum width/length 0.10-0.13 (mean = 0.12, $n = 6$) including the epiphallus, which varies from being straight and weakly-defined (Fig. 23) to distinct and bent (Fig. 25); without appendix or flagellum; penial retractor muscle terminal. Vas deferens narrow, expanding proximally from approximately mid-length to reach its maximum diameter (about 2-3 times its minimum diameter) at the junction with the prostate gland. Internally, the penis bears two fleshy pilasters developed into lobes or lamellae in the mid-penis (Figs. 23a, 24). In the terminal penis the pilasters are weakly developed, thus defining the epiphallus, and extend into the vas deferens as weakly-defined ridges of the thickened epiphallar wall (Fig. 23a); towards the base of the penis the pilasters are low ridges that extend into the atrium and vagina (Fig. 23a). No papillae, glandulose regions, colored regions, or other additional features were visible at the magnification used (40X).

Comparison with related species

Daedalochila bisontes conforms to the *Polygyra plicata* group of Polygyridae on the basis of its depressed, openly umbilicate shell; triangular-quadrate parietal tooth with a callus appressed to the body whorl; the presence of basal and palatal lamellae; and its geographical localization (Pilsbry 1940: 625).

In general aspect, *Daedalochila bisontes* most closely resembles *Daedalochila peregrina* (Figs. 19-22); that is, the rounded periphery, open umbilicus, and deeply placed palatal lamella. On casual inspection the parietal lamella of *D. bisontes* resembles that of *D. peregrina*, but the prominent projection on the apical side and the angle basally (Figs. 3-4, 6-9) are constant features of all known adult specimens of *D. bisontes* and are not features that develop only in gerontic individuals of the species. Figs. 8 and 9 represent the range of variation of shape of the parietal lamella in the paratype series. The parietal lamella of *D. peregrina* has only an irregularity on the apical side, where it bends into the aperture; the basal side is straight or slightly curved (Figs. 20-21 and see Pilsbry 1940, Fig. 397:9). The two species are distinguished further by the generally smaller size of *D. bisontes*, the more closely coiled whorls, and the greater number of umbilical whorls (Figs. 40-41). In contrast to *D. peregrina*, *D. bisontes* shows weak rib striation that is present on the apical surface only (and behind the aperture) (Figs. 1-5). Although striation is regarded as a variable feature (for example, in *Daedalochila fatigiata* [Pilsbry 1940: 628-629] and *Daedalochila dorfeuilliana* [Pilsbry 1940: 634-637, 633, fig. 398]), this

is a constant difference between all known specimens of *D. bisontes* and all the *D. peregrina* that we have examined.

In the form of the parietal lamella *Daedalochila bisontes* bears some resemblance to *Daedalochila plicata* (Pilsbry 1940, Fig. 397:1), *Daedalochila fatigiata* (Pilsbry 1940, Fig. 397:4) and *Daedalochila troostiana* (Pilsbry 1940, Fig. 397:8), which also possess a projection on the apical side of the parietal lamella and an obtuse angle on the basal side. However, the deeply immersed and long palatal lamella curving inwards and downwards into the body whorl towards the basal lamella distinguishes *D. bisontes* from *D. troostiana*, *D. fatigiata*, *D. dorfeuilliana*, *Daedalochila lithica* (Hubricht, 1961) and *Daedalochila mooreana* (W.G. Binney, 1857) (also from *Linisa texasiana* [Moricand, 1833] and related species). This feature is most clearly seen by viewing the lamellae from "behind" the aperture after removal of the body whorl. Figs. 10-18 illustrate such views for all the well-defined species of the *Polygyra plicata* group and for *Daedalochila mooreana*, the type species of *Millerelix*. The palatal lamella is usually visible externally as a whitish line that forms an arc that defines a smooth, raised area behind the peristome. For examples, see Pilsbry 1940: pp. 632 & 627, Fig. 397:14 (*Daedalochila jacksoni*); pp. 626-627, Fig. 397:1 (*D. plicata*); p. 631 and Fig. 22 of this report (*D. peregrina*); and Fig. 5 of this report (*D. bisontes*). *D. plicata* lacks an internal tubercle on the umbilical suture, the basal lamella extends into the body whorl to reach the umbilical suture (Fig. 14) (see also Pilsbry 1940: 626-627), and is also distinct in internal morphology of the penis (see below). *D. jacksoni* has a palatal lamella very similar to that of *D. bisontes* (compare Figs. 10 and 12), but in general form, the shell of *D. jacksoni* presents a very different aspect, being more inflated with a rounded base, and possessing a higher spire and a short umbilical suture (Pilsbry 1940, Fig. 397:11-15). *D. jacksoni* is further distinguished by the strong tongue-like parietal lamella, the lack of an internal tubercle, and the morphology of the penis (see below).

An apparently unique feature of *Daedalochila bisontes* is the appearance of the palatal lamella as two overlapping lamellae when viewed through the aperture. This arises because the tooth is sinuous and undulate, being high at its outer and inner ends, with a low mid-portion so that only the two higher portions are visible through the aperture. This feature is easily seen with shells "in the hand" where light and angle can be readily manipulated, but is not well defined in Figures 3, 4, and 6-9 because of difficulties of lighting and limitation of depth of field. Figure 11 shows this aspect viewed from behind the aperture. This feature is absent in *Daedalochila peregrina*, which possesses a palatal lamella that becomes more uniformly low toward the body whorl (Fig. 13), thus further distinguishing *D. peregrina* and *D. bisontes*. In *Daedalochila jacksoni* the inner end of the

palatal lamella (viewed through the aperture) is obscured by the strong parietal lamella (see Pilsbry, 1940, Fig. 397:11-14).

In practice, specimens of *Daedalochila bisontes* can be identified without recourse to opening the shell by the combination of rounded periphery, open and almost planar umbilical spiral, the weak striation that is obsolete below the periphery, and the projections on the parietal lamella. Identity can be confirmed by examining the structure of the palatal lamella as viewed through the aperture and behind the peristome.

Distribution

The localities to date are in a restricted area close to the Buffalo River region of the Ozark Mountains of Arkansas, U.S.A. All sites are on limestone outcrops. Thus, *Daedalochila bisontes* appears to represent an Arkansas-Ozarkian endemic species. Several other species of Polygyridae that are either endemic to Arkansas or are of restricted distribution are also known from this area (Hubricht 1985, Coles and Walsh 1999, Walsh and Coles 2002), namely *Daedalochila peregrina*, *Patera clenchi* (Rehder, 1932), and *Triodopsis neglecta* (Pilsbry, 1899). At the type locality, *D. bisontes* was found sympatric with *Daedalochila dorfeuilliana*. A single lot (FMNH267965: Arkansas, Stone County, White River, 0.5 miles N of Allison, L. Hubricht, 2 September 1960) contained *D. peregrina*, *Daedalochila jacksoni*, and *D. bisontes* (these last recataloged as FMNH287400). We have seen only *D. peregrina* and *D. dorfeuilliana* from this area and Hubricht (1985) does not report Stone County, Arkansas, for *D. jacksoni*. *D. bisontes* appears to have been overlooked because of its superficial similarity to small specimens of *D. peregrina*.

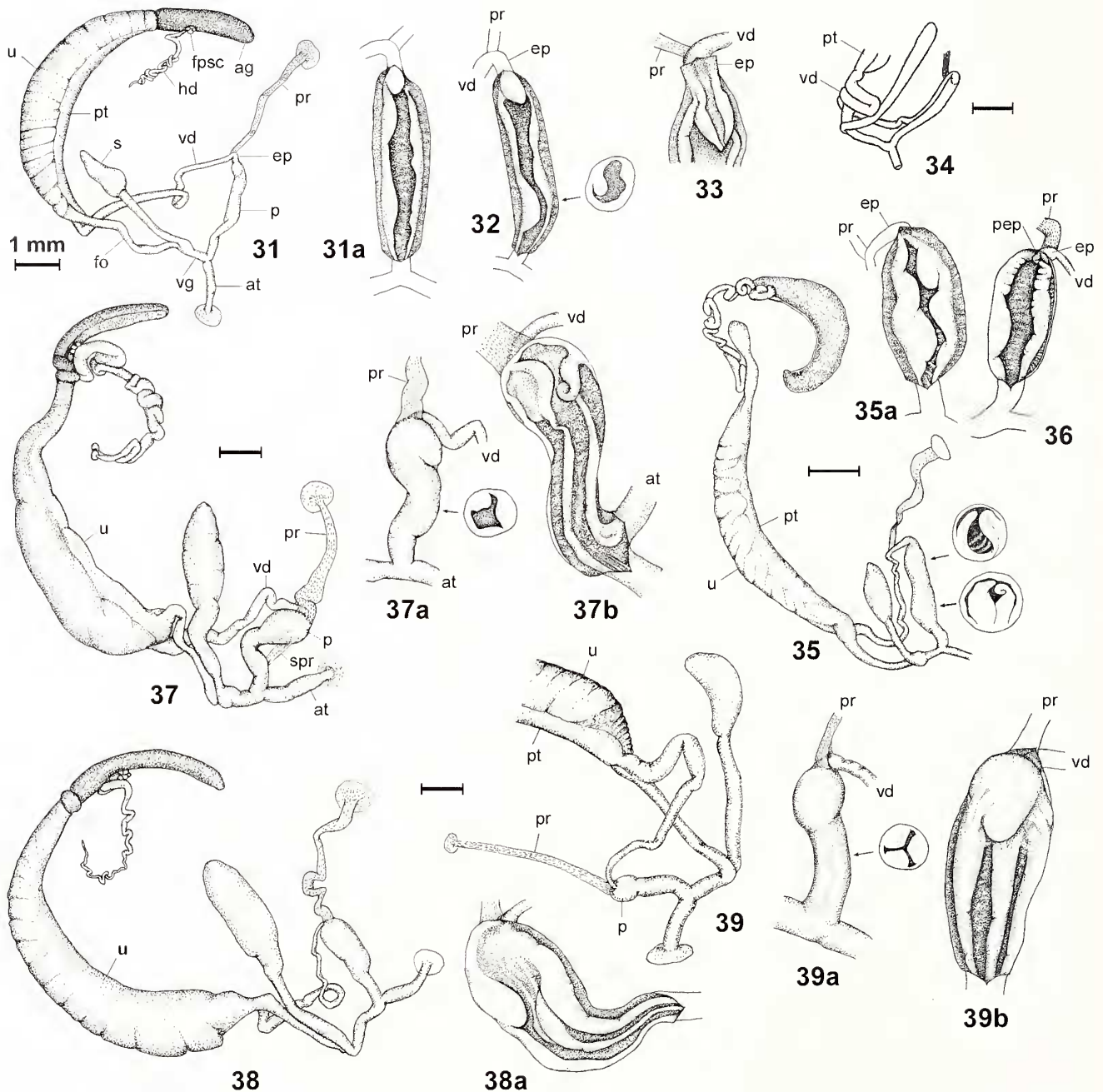
Etymology

The specific epithet *bisontes* is derived from the early modern English word for bison and refers to the known localities in the region of the Buffalo National River of Arkansas. The vernacular name *Buffalo River liptooth* is proposed for the species.

GENITAL ANATOMY OF THE POLYGYRA PLICATA GROUP

General features

The genitalia of all specimens dissected were of the general form described for *Daedalochila bisontes*. That is, in the approximate relative proportions of the atrium, vagina, penis, and free oviduct; the attachment of the penial retractor muscle at the apex of the penis; the lack of flagellum or appendix; and the thickening of the proximal vas deferens at its junction with the prostate gland. Differences between species, particularly with respect to the shape of the penis, its



Figures 31-39. Genital anatomy of *Daedalochila plicata*, *Daedalochila dorfeuilliana*, *Daedalochila troostiana*, and *Daedalochila fatigiata*. Fig. 31, *Daedalochila plicata*, genital anatomy; Fig. 31a, opened penis of same specimen. Fig. 32, *D. plicata*, opened penis of a second specimen and section of the penis (inset). Fig. 33, *D. plicata*, details of the apical pendant conical projection of the penis in a third specimen (viewed from opposite side of penis compared to Figs. 31a, 32). Fig. 34, *D. plicata*, distal genitalia of a fourth specimen in a less disturbed state. Fig. 35, *Daedalochila dorfeuilliana*, genital anatomy and sections of the penis (insets); Fig. 35a, penis of the same specimen opened from near the vagina/atrium to the epiphallus. Fig. 36, *D. dorfeuilliana*, penis of a second specimen showing the junction of the penis and epiphallus, puckering of the pilasters, and puckering of the epiphallar walls (pep). Fig. 37, *Daedalochila troostiana*, genital anatomy showing secondary penial retractor muscle (spr); Fig. 37a, enlarged view of penis of the same specimen showing penial retractor muscle enveloping base of the vas deferens and section of the penis (the secondary penial retractor muscle is omitted for clarity); Fig. 37b, opened penis of the same specimen. Fig. 38, *Daedalochila fatigiata*, genital anatomy; Fig. 38a, penis of the same specimen opened to the vas deferens. Fig. 39, *D.*

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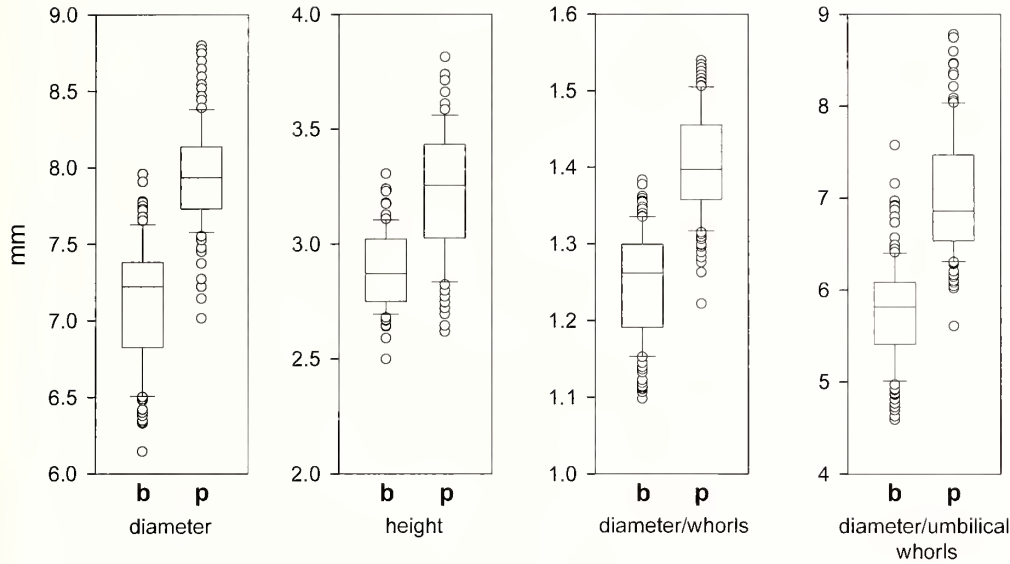


Figure 40. Box plots of variation of shell size and coiling in *Daedalochila bisontes* sp. nov. and *Daedalochila peregrina*. The boxes represent the 25th-75th percentiles of data and the bars the 10th-90th percentiles, data outside of these ranges are represented by circles, and the lines within the boxes illustrate the median. **b**, *D. bisontes*, **p**, *D. peregrina*. Student's t-test generates $p < 0.001$ for differences of the means of these measurements for the species pairs in all four graphs.

internal features, and the degree of development of the epiphallus, are given below and summarized in Table 2.

Daedalochila peregrina (Rehder, 1932)
(Figs. 26-28)

FMNH293230: Arkansas, Searcy County, Highway 65 opposite junction with Highway 74, approximately 6 miles NW of Marshall, B. Coles, 21 April 2002. Six specimens dissected, penis opened in 3 specimens.

The penis is approximately cylindrical, maximum width/length 0.15-0.19 (mean = 0.17, $n = 3$); the epiphallus short and ill defined (Fig. 26). The vas deferens is thickened proximally, maximally thickened at the junction with the prostate gland (approximately 2-3 times its minimum diameter). Internally, the penis bears two pilasters that run the entire length and which are developed into low (Fig. 27) or broad (Fig. 26a) fleshy ridges that are variously branched and anastomose. One pilaster passes into the vas deferens as a low ridge. No glandular or colored areas were visible at the magnification used (40X).

The penis differs from that of *Daedalochila bisontes* in being more uniformly cylindrical, with a short, ill-defined

epiphallus and the pilasters being low, variously branched, and fused.

Daedalochila jacksoni (Bland, 1866)
(Figs. 29-30)

FMNH293236: Arkansas, Benton County, Hobbs Wildlife Management Area, G. Walsh, 26 January 2003. Three specimens dissected including opening of the penis.

The penis has a narrow base, widens at mid-length, and narrows before a distinct, swollen apex, maximum width/length 0.14-0.17 (mean = 0.15, $n = 3$) and does not possess an epiphallus (Figs. 29, 30). The vas deferens is thickened proximally, strongly (and maximally) thickened at the junction with the prostate gland (approximately 3-4 times the minimum diameter). Internally, the penis has two pilasters strongly developed at the penial apex into high, fleshy lamellae; apically, the pilasters appear to fuse with the walls of the vas deferens (Fig. 29a, 30a). No glandular or colored areas were visible at the magnification used (40X). The atrium was relatively longer than observed for *Daedalochila bisontes*, approximately 2/5 the length of the penis.

The penis differs from that of *Daedalochila bisontes* in

Figures 31-39. (continued)

fatigiata, distal genitalia of a second specimen; Fig. 39a, enlarged view of the penis of the same specimen showing penial retractor muscle enveloping the base of the vas deferens and section of penis (inset); Fig. 39b, penis of the same specimen showing strongly developed pilasters and apical complex (in a less disturbed state than in Fig. 38a); the features between the vas deferens and the apical penial complex of Fig. 39b are due to ripping of the tissues during dissection. Scale bars are all 1 mm and refer to the gross genitalia only. Abbreviations: ag, albumin gland; at, atrium; ep, epiphallus; fo, free oviduct; fp, fertilization pouch-seminal receptacle complex; hd, hermaphrodite duct; p, penis; pep, puckered epiphallus at junction with penis; pr, penial retractor muscle; pt, prostate gland; s, spermatheca; spr, secondary penial retractor muscle; u, uterus; vd, vas deferens; vg, vagina.

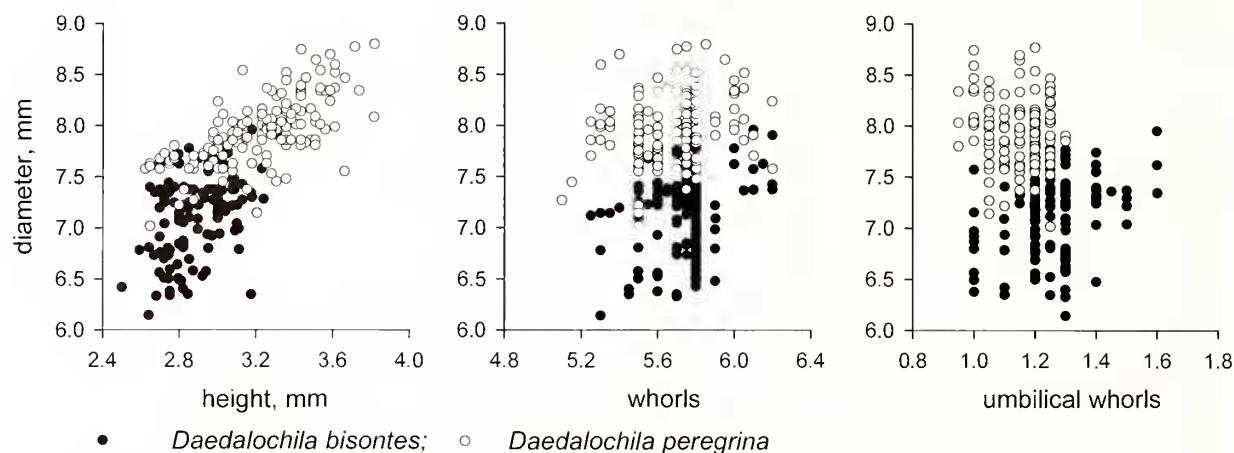


Figure 41. Discrimination of *Daedalochila bisontes* and *Daedalochila peregrina* on the basis of size and coiling. Shell diameter has been plotted against shell height, whorl number, and umbilical whorl number for each measured shell.

possessing a distinct, swollen apex corresponding to the strong development of the pilasters in the apex of the penis.

Daedalochila plicata (Say, 1821)
(Figs. 31-34)

FMNH293238: Alabama, Jackson County, County Road 33, approximately 5 miles E of Skyline, B. Coles, 18 April 1999. Three specimens dissected, including opening of the penis.

The penis is cylindrical, maximum width/length 0.11-0.12 (mean = 0.12, $n = 3$), with a short epiphallus. The vas deferens is thickened proximally, reaching its maximum diameter (approximately 3 times its minimum diameter) at the junction with the prostate gland (Fig. 34). Internally, the penis bears two pilasters that are variously developed

into low lamellae. Apically, the pilasters fuse with a pendant conical projection that accurately defines the beginning of the epiphallus (Figs. 31a-33). In detail, this consists of extension of the walls of the vas deferens into the penial lumen; the thickened walls being rolled inwards (Fig. 33) (note that in the less disturbed state, the in-rolled margins are in contact with each other). No glandular or colored areas were visible at the magnification used (40X). The atrium was relatively longer than in *Daedalochila bisontes* (approximately 1/2 the length of the penis) and the vagina was shorter.

Daedalochila plicata differs from all other species of the *Polygyra plicata* group by the presence of the apical pendant conical projection and the short but well-defined epiphallus.

Table 2. Summary of the morphology of the penis and vas deferens for the *Polygyra plicata* group¹ as observed by the authors.

	<i>D. plicata</i>	<i>D. bisontes</i>	<i>D. dorfeuilliana</i>	<i>D. peregrina</i>	<i>D. jacksoni</i>	<i>D. fatigiata</i>	<i>D. troostiana</i>
1. pendant conical projection in penis	present	absent	absent	absent	absent	complex	complex
2. penis width/length	~0.12	~0.12	~0.15	~0.17	~0.15	~0.34	~0.38
3. epiphallus	short, well-defined	variable	distinct, reflexed	short, ill-defined	absent	absent	absent
4. thickening of proximal vas deferens (vd)	~3X	~2-3X	~2-3X	~2-3X	~3-4X	~4X	~2X (thick throughout)
5. apex of penis	simple	variable	bent	simple	complex	simple, but enlarged	simple, but enlarged
6. pilasters	2	2	2	2	2	3	2
7. penial retractor muscle	apical	apical	apical	apical	apical	envelops distal vd	envelops distal vd

¹ All species of the group are here included in the genus *Daedalochila*.

Daedalochila dorfeuilliana (Lea, 1838)
(Figs. 35-36)

FMNH293240: Arkansas, Hempstead County, Lake Millwood at Saratoga Landing, B. Coles, 5 January 2003. Six specimens dissected, penis opened in 4 specimens. *D. dorfeuilliana sampsoni* (Wetherby, 1881). FMNH293241: Arkansas, Marion County, Buffalo Point, 3 miles E of Mull, B. Coles, 20 January 2003. One dissected including opening of the penis.

The penis is narrow basally, thickened in mid-region and contracted into a reflexed epiphallus, maximum width/length 0.09-0.19 (mean = 0.15, $n = 4$). The vas deferens is thickened proximally, reaching its maximum diameter (approximately 2-3 times its minimum diameter) at the junction with the prostate gland. Internally, the penis bears two pilasters that are variably thickened into lamellae and lobes. These form low ridges basally and apically, and apically appear to extend into the epiphallus (Fig. 35a). One specimen had a short and stout epiphallus (Fig. 36). In this example, the pilasters were seen to be puckered apically and contiguous with the thickened and puckered tissues around the junction of the epiphallus and penial lumen. One fold of the puckered epiphallus was prominent, corresponding to the pilaster passing into the epiphallus.

The single specimen of the form *sampsoni* did not differ anatomically from the nominal form.

The general form of the penis of *Daedalochila dorfeuilliana* is similar to that of *Daedalochila bisontes*; however, the lobes of the pilasters are more strongly developed apically.

Daedalochila troostiana (Lea, 1839)
(Figs. 37, 37a, 37b)

FMNH293242: Tennessee, De Kalb County, Cove Hollow Road at N end of Center Hill Lake, B. Coles, 16 April 1999. One dissected including opening of the penis.

The penis is stout, narrower basally, thickened terminally, maximum width/length 0.38, without any trace of epiphallus. The penial retractor muscle is broad and envelops the penial apex and the penial end of the vas deferens (Fig. 37a). A very fine sheet-like secondary retractor muscle connects the terminal and basal penis (Fig. 37). The vas deferens is thickened throughout, becoming greatly thickened at the junction with the prostate gland (approximately twice its minimum diameter). Internally, the penis bears two pilasters that extend as low ridges into the vagina and atrium (Fig. 37b). Terminally, these fuse with a complex of folds and thickened tissue that is contiguous with the walls of the penis, and which appears to fuse with the thickened walls of the vas deferens (Fig. 37b). The atrium is relatively long, approximately half the length of the penis.

Daedalochila fatigiata (Say, 1829)
(Figs. 38-39)

FMNH293245: Tennessee, Perry County, Mousetail Landing State Park, Perryville, B. Coles, 24 March 2000. Four dissected, penis opened in two specimens. (The form is *Daedalochila fatigiata internuntia* [Pilsbry, 1940] on the basis of distinct rib striation below the periphery of the shell).

The penis is narrow basally, thickened terminally, maximum width/length 0.32-0.36 (mean = 0.34, $n = 4$), without any trace of epiphallus. The penial retractor muscle envelops the apex of the penis and the penial end of the vas deferens (Fig. 39a). The vas deferens widens proximally to reach its maximum diameter (approximately 4 times its original diameter) at the junction with the prostate gland. Internally the penis bears three pilasters that are narrow basally and become strong at mid-length where they are developed into lamellae. In the terminal penis, these fuse with a series of complex folds and thickened tissue that is contiguous with the penial walls, one part of which forms a prominent lobe; this complex appears to fuse with the thickened walls of the vas deferens (Figs. 38a, 39b). The atrium is relatively long, approximately half the length of the penis.

Daedalochila troostiana and *Daedalochila fatigiata* differ from other members of the *Polygyra plicata* group in the combination of a thicker penis that is markedly swollen at the apex, the complete lack of an epiphallus, the penial retractor muscle enveloping the vas deferens at its junction with the penis, and the complex series of folds and thickened tissue in the apical region of the penis.

DISCUSSION

The most recent studies of the Polygyridae are those of Emberton (1988, 1991, 1995), who, on the basis of detailed studies and summaries of previous work, established clades defined by shared characters regardless of their subsequent evolutionary modification. The resultant taxonomy differs in many respects from that of Pilsbry (1940) which, until that time, was the most authoritative study of the family. Pilsbry included all the depressed, umbilicate species of the Polygyridae in which the peristome is connected by a raised parietal callus or a V-shaped parietal lamella, into a single genus, *Polygyra* Say, 1818. The species having only a parietal lamella were placed in the subgenus *Polygyra sensu stricto* and the remaining species with parietal, basal, and palatal lamellae were placed in the subgenus *Daedalochila* Beck, 1837. Emberton (1995) treated *Polygyra*, *Daedalochila*, and Pilsbry's sections of *Daedalochila* (*Linisa* Pilsbry, 1930 and *Lobosculum* Pilsbry, 1930) at full generic status. However, Emberton's most substantive departure from Pilsbry's treatment was to include these four genera; *Praticolella* Martens, 1892; and *Giffordius* Pilsbry, 1930 in a tribe, the Polygyrini

sensu stricto, and to bring *Praticolella*, *Linisa* (in part), and *Lobosculum* (in part) together as a clade on the basis of the anatomy of the penis (a sacculate glandular diverticulum of the lower penis), despite their dissimilar shells. Pilsbry's (1940) concept of *Daedalochila* (with the exception of *Linisa* and *Lobosculum*, as mentioned above) was retained by Emberton in the form of a clade defined by "a vestigial epiphallus without a flagellum" and preceding characters that define the tribe (Emberton 1995: 77, characters 70-74, 86). The character states used by Emberton to define genera and subgenera within this clade and his assignment of species are summarized in Table 1. This arrangement is based on limited anatomical information. For *Millerelix*, anatomy has been illustrated only for *Millerelix* (*Millerelix*) *mooreana* (Pratt 1981a: 30, fig. 4), *Millerelix* (*Millerelix*) *dorfeuilliana* (Pratt 1981a: 44, fig. 8), and *Millerelix* (*Prattelix*) *plicata* (Emberton 1995: 80, fig. 4. (Pratt's figures 4 and 8 are also reproduced in Emberton 1995: 81, fig 5.) (Rehydrated material of *Millerelix* [*Millerelix*] *gracilis* [Hubricht, 1961] was also examined by Pratt [1981a].)

Pratt established *Millerelix* on the basis of the genital anatomy of *Millerelix mooreana* and *Millerelix dorfeuilliana* and, in fact, explicitly excluded *Polygyra plicata* from the genus (Pratt 1981a: 27). Emberton extended the concept to include all the members of the *Polygyra plicata* group because of the presence of "an apical, pendant, conical projection" in the penis of *Polygyra plicata*. Pratt did not indicate whether he observed this feature for *Polygyra plicata* and, if so, whether he regarded it as being homologous with that described in his diagnosis of *Millerelix* "the very short epiphallus enters the penis through a short tubular verge" (Pratt 1981a: 25). Emberton qualified his revised description of this diagnostic feature of *Millerelix* to say "and derivatives thereof" presumably to allow extension of Pratt's concept of *Millerelix* to include *Polygyra plicata*.

It is against this background that we compare our dissections of *Daedalochila plicata* and *Daedalochila dorfeuilliana* with published illustrations and discuss the newly presented anatomy of *Daedalochila bisontes*, *Daedalochila fatigiata*, *Daedalochila jacksoni*, *Daedalochila peregrina*, and *Daedalochila troostiana*.

Our dissections of *Daedalochila* (*Millerelix* [*Prattelix*]) *plicata* agree with that of Emberton (1995), both in form and dimensions, notably the relative width/length of the penis (0.12) and the thickening of the proximal vas deferens. The vas deferens at its junction with the prostate gland was approximately three times its minimum diameter in both Emberton's and our specimens; however, it appears more stout throughout in Emberton's illustration (Emberton 1995: 80, fig. 4). The apical, pendant, conical projection was a prominent feature of all specimens. This feature appears to be an extension of the vas deferens into the penial lumen and,

although not tubular, otherwise appears to conform to Pratt's diagnosis of *Millerelix*.

In contrast, our dissections of *Daedalochila* (*Millerelix* [*Millerelix*]) *dorfeuilliana* bear little resemblance in detail to those of Pratt. Specimens that we dissected had shorter penises and the proximal vas deferens were thickened at their junctions with the prostate gland. The length of the penis in each of our specimens (approximately 2.5 mm) was almost half that of Pratt's specimen (4.0 mm), although the width (0.4 mm) was similar (Pratt, 1981a: 43). The internal anatomy of the penis agrees with Pratt's description in the presence of two longitudinal pilasters, but the diagnostic generic character of a *tubular verge* was not seen in any of our specimens. In fact, Pratt indicated that this is a variable feature in *Millerelix dorfeuilliana*, stating that "in a relaxed specimen . . . the verge is short, reduced to a p[a]pilla" (Pratt, 1981a: 43), even though for the same specimen it is illustrated as a prominent feature and drawn as if of greater size than in *Millerelix mooreana* (Pratt 1981a, figs. 4 and 8).

These data suggest that compared to Pratt's material, our material was subject to contraction during preservation (even though both sets of material were apparently preserved in a similar way); preservation method being known to result in changes in tissue dimensions (Emberton 1989). Nevertheless, because all our material was preserved in the same way, because museum material is usually preserved using the same method as that used by us, and because the anatomy of our specimens of *Daedalochila plicata* closely resemble that of Emberton (1995), we feel that comparisons within our material and with other published dissections are meaningful.

A comparison of the diagnostic generic and subgeneric characters within the *Daedalochila*/*Millerelix* clade as used by Emberton (1995) (Table 1) and as observed by us for the members of the *Polygyra plicata* group (Table 2) indicate the following:

1. *An apical pendant conical projection in the penis* was seen only in *Daedalochila plicata*, presents a different form in *Daedalochila troostiana* and *Daedalochila fatigiata*, was not confirmed for *Daedalochila dorfeuilliana*, and is absent in *Daedalochila bisontes*, *Daedalochila peregrina*, and *Daedalochila jacksoni*.
2. *Penis width/length*. For *Daedalochila plicata*, *Daedalochila bisontes*, *Daedalochila dorfeuilliana*, *Daedalochila peregrina*, and *Daedalochila jacksoni*, the width/length of the penis is within (or close to) the limit defining *Millerelix*. For *D. dorfeuilliana* (*Millerelix* [*Millerelix*]) the ratio is approximately twice than that given for *Millerelix* (*Millerelix*) and does not appear to be different from that of *D. plicata* (*Millerelix* [*Prattelix*]). For *Daedalochila troostiana* and

Daedalochila fatigiata, this ratio is considerably greater than that defined for *Millerelix*, greater than that for *D. plicata*, *D. bisontes*, *D. dorfeuilliana*, *D. peregrina*, and *D. jacksoni*, and similar to that for *Daedalochila (Upsilidon)*.

3. *Epiphallus*. An epiphallus is a well-defined feature of *Daedalochila plicata*, variable in development or ill-defined for *Daedalochila dorfeuilliana*, *Daedalochila bisontes* and *Daedalochila peregrina*, and absent in *Daedalochila jacksoni*, *Daedalochila troostiana*, and *Daedalochila fatigiata*.
4. *Thickness of proximal/distal vas deferens*. All species showed a thickened proximal vas deferens and this feature was not markedly different between *Daedalochila dorfeuilliana* (*Millerelix* [*Millerelix*]) and *Daedalochila plicata* (*Millerelix* [*Prattelix*]).
5. The *apex of the penis* is variable between species (and defined by the shape of the pilasters and other internal features).
6. The *penial pilasters* vary in number from two to three.
7. The *penial retractor muscle* envelops the distal vas deferens in *Daedalochila fatigiata* and *Daedalochila troostiana* (and a secondary retractor muscle is present in at least *D. troostiana*).

Thus, the characters used to define *Millerelix sensu* Emberton are not consistently present in the *Polygyra plicata* group and do not adequately address the variation between the species included by Emberton in *Millerelix*. Conclusions based on these new data and the published illustrations referred to above are as follows:

1. The presence of a pendant conical projection in the apical penis varies between the species, and/or appears to vary between individuals (*Daedalochila dorfeuilliana*), or is dependent on the methods of preservation (*D. dorfeuilliana*).
2. The width/length of the penis does not differentiate between *Millerelix* (*Millerelix*) (*Daedalochila dorfeuilliana*) and *Millerelix* (*Prattelix*) (*Daedalochila plicata*), and may be an unreliable character because of variation between individuals of the same species or contraction during preservation.
3. The thickening of the proximal epiphallus at its junction with the prostate gland does not differentiate between *Millerelix* (*Millerelix*) and *Millerelix* (*Prattelix*) and is a variable feature, possibly subject to differences between individuals of the same species and changes during preservation.
4. Several features of Pilsbry's *Polygyra plicata* group appear to be common to *Daedalochila sensu* Emberton, that is, the complete lack of an epiphallus in

Daedalochila jacksoni, *Daedalochila troostiana*, and *Daedalochila fatigiata* and the stout penis of *D. troostiana* and *D. fatigiata*.

Because of this we feel that, when this novel anatomical information is included, the diagnostic characters of *Millerelix* and *Daedalochila* are shown to be unreliable for defining clades. Thus, the species included in *Millerelix sensu* Emberton (1995) should revert to the senior genus *Daedalochila* Beck, 1837. That is, the *Millerelix/Daedalochila* clade of Emberton (1995) is assigned the generic rank of *Daedalochila*. *Daedalochila* has been used in this sense in this study.

Despite this conclusion, it is not our intention to imply that *Daedalochila* should not be separated into multiple genera or subgenera. For example, *Daedalochila sensu stricto* and *Upsilidon* Pilsbry, 1940 were originally defined on the basis of shell characters, that is, the ear-shaped parietal lamella and raised parietal callus of *Daedalochila* (*Daedalochila*) (Pilsbry 1940: 592) and the U-shaped parietal lamella of *Daedalochila (Upsilidon)* (Pilsbry 1940: 637).

Several shell features that have potential as diagnostic subgeneric characters are also present in the *Polygyra plicata* group. For example, *Daedalochila bisontes*, *Daedalochila jacksoni*, and *Daedalochila peregrina* have in common a deeply immersed, long, and curved palatal lamella (Figs. 10-13); and *Daedalochila troostiana* and *Daedalochila fatigiata* are closely similar in apertural features (Figs. 15-16). However, the relationship between shell features and anatomical features within *Daedalochila* are poorly known and the species of the genus require further study before reliable subgeneric status can be assigned. Notably, the anatomical relationship of *D. troostiana* and *D. fatigiata* with *Upsilidon* should be examined, and the consistency of the internal features of the penis of *Daedalochila dorfeuilliana* and its relationship to *Daedalochila mooreana* need to be reexamined. Similarly, the newly observed anatomical features of Table 2 need to be included in any novel cladistic or systematic analyses of the genus.

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LITERATURE CITED

- Coles, B. F. and G. E. Walsh, 1999. A revised list of Arkansas terrestrial mollusks with notes on the geographic distribution of species. *Journal of the Arkansas Academy of Sciences* **53**: 32-37.
- Emberton, K. C. 1988. The genitalic, allozymic, and conchological evolution of the eastern North American Triodopsinae (Gastropoda: Pulmonata: Polygyridae). *Malacologia* **28**: 159-273.
- Emberton, K. C. 1989. Retraction/extension and measurement errors in a land snail: Effects on systematic characters. *Malacologia* **31**: 157-173.
- Emberton, K. C., 1991. The genitalic, allozymic and conchological evolution of the tribe Mesodontini (Pulmonata: Stylommato-phora: Polygyridae). *Malacologia* **33**: 71-178.
- Emberton, K. C. 1995. When shells do not tell; 145 million years of evolution in America's polygyrid land snails, with a revision and conservation priorities. *Malacologia* **37**: 69-110.
- Hubricht, L. 1985. The distributions of the native land mollusks of the eastern United States. *Fieldiana, Zoology (New Series)* **24**: 1-191.
- Pilsbry, H. A. 1939. *Land Mollusca of North America (North of Mexico)*, Vol. 1, Part 1. The Academy of Natural Sciences of Philadelphia, Philadelphia.
- Pilsbry, H. A. 1940. *Land Mollusca of North America (North of Mexico)*, Vol. 1, Part 2. The Academy of Natural Sciences of Philadelphia, Philadelphia.
- Pratt, W. L. 1981a. *A Revision of the Land Snail Genus Polygyra in Texas*. Ph.D. Dissertation, University of Arizona, Tucson.
- Pratt, W. L. 1981b. A revision of the land snail genus *Polygyra* in Texas. *Dissertation Abstracts International* **42**: 1352-B.
- Turgeon, D. D., J. F. Quinn Jr., A. E. Bogan, E. V. Coan, F. G. Hochberg, W. G. Lyons, P. M. Mikkelsen, R. J. Neves, C. F. E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F. G. Thompson, M. Vecchione, and J. D. Williams. 1998. *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada, Mollusks*, 2nd Ed. American Fisheries Society, Special Publication 26. American Fisheries Society, Bethesda, Maryland.
- Walsh, G. E. and B. F. Coles, 2002. Distributions and geographical relationships of the polygyrid land snails (Mollusca, Gastropoda, Polygyridae) of Arkansas. *Journal of the Arkansas Academy of Sciences* **56**: 212-219.